NOTES ON THE VEGETATIVE ANATOMY OF ARISTEYERA SPICATA (PALMAE) [1]

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THE FOLLOWING ACCOUNT OF THE ANATOMY of leaf and stem of *Aristeyera spicata* H. E. Moore forms an appendix to the taxonomic description by Dr. Moore and the study of the morphology and anatomy of the inflorescence axis and flowers by Mrs. Uhl being published simultaneously with this paper.[2]

MATERIAL AND METHODS

Small dried fragments of leaf-blade, petiole, and stem, without precise indication of their position, from the type collection (*Steyermark 90010*) were available for study. Material of the lamina was revived, and preparations in which the surface layers and internal tissues could be studied in various planes were made according to techniques outlined in Tomlinson, 1961 (p. 4). Dried fragments of petiole and stem were infiltrated directly with celloidin solvent (ethanol : ether in equal volumes) under a slight vacuum. Celloidin impregnation involved transference through a graded series of celloidin solutions (2–12%) in a 60° C oven in tightly stoppered bottles. Longitudinal and transverse sections of the hardened celloidin blocks were cut on a Reichert sliding microtome. Maceration of tissues with 10% KOH and 20% chromic acid provided isolated elements, particularly of the xylem. Most observations and drawings were made from sections mounted in glycerine; some permanent preparations stained in safranin and Delafield's haematoxylin were also examined.

ANATOMY

Lamina. Dorsiventral. Adaxial epidermis smooth; abaxial epidermis prominently ribbed, ribs irregularly spaced and with a graded series from largest, prominent ribs to large veins of lamina not producing ribs (FIGS. 12 and 18–21). Margin ribbed (FIG. 11). HAIRS (FIGS. 3, 9, 10, 24, 25) restricted to costal regions, most frequent below large ribs, least frequent in adaxial costal regions; solitary, irregularly scattered or rarely in pairs.

[1] This study has been carried out with support from the National Science Foundation, Grant GB-506.

[2] MOORE, H. E. *Aristeyera*, a new genus of Geonomoid Palms. Jour. Arnold Arb. **47**: 1–8. 1966.

UHL, N. W. Morphology and anatomy of the inflorescence axis and flowers of a new palm, *Aristeyera spicata*. Jour. Arnold Arb. **47**: 9–22. 1966.

Each hair a more or less uniseriate adpressed filament, always pointing distally, not or scarcely sunken, arising from a single epidermal cell; basal cells conspicuously pitted, slightly lignified with a transition to thin-walled, delicate distal cells; filament probably much longer in immature leaves, but shortened in mature leaves by disappearance of terminal ephemeral cells. Adaxial somewhat thicker-walled than abaxial hairs, tending to become multiseriate by transverse segmentation of filament cells. ADAXIAL EPIDERMIS (FIG. 1) uniform, cells above veins not or scarcely differentiated from those elsewhere; cells in longitudinal files but markedly obliquely extended, more or less rhombohedral in surface view, without sinuous walls. Outer wall somewhat thicker than remaining walls with a thin cutinized layer penetrating somewhat between anticlinal walls. ABAXIAL EPIDERMIS somewhat shallower and thinner-walled than adaxial (14–15μ compared with 20–22μ); subdivided irregularly into costal bands of varying width below veins (FIG. 3) and wider intercostal bands (FIG. 2) between veins. Costal cells more or less rectangular in surface view, smaller than intercostal; intercostal cells obliquely extended but more irregular than adaxial cells. STOMATA (FIGS. 2 and 6–8) restricted to abaxial surface, diffusely distributed in intercostal regions, not in distinct longitudinal files. Terminal subsidiary cells somewhat shorter than, but otherwise not differentiated from normal epidermal cells. Lateral subsidiary cells wide, thin-walled and more conspicuously distinguished from remaining epidermal cells. Guard cells not sunken, equal in depth to abaxial epidermis, each with two prominent cutinized ledges (FIG. 8). Wall beneath ledges somewhat thickened; cell lumen wide and otherwise unrestricted (FIG. 7). EXPANSION CELLS developed as longitudinal bands of enlarged cells at intervals below each surface (FIG. 21 *exp.*). COLORLESS HYPODERMIS absent adaxially; represented beneath abaxial surface by a compact layer of thin-walled, colorless, more or less cubical cells (FIG. 13), those below largest veins smaller than cells elsewhere. Hypodermis interrupted by wide substomatal chambers each surrounded by 4 cells appearing more or less L-shaped in surface view (FIG. 4). ASSIMILATING MESOPHYLL without distinct palisade layers; adaxial cells compact (FIGS. 5, 14), somewhat transversely extended; middle mesophyll layers looser, aggregated into indistinct transverse diaphragms, forming a well-developed intercellular space system obvious only in longitudinal sections (cf. FIGS. 13 and 14). FIBERS up to 18μ wide, with wide septate lumina, unlignified walls; abundant throughout mesophyll, most common in adaxial layers; solitary or 2–3 forming narrow fibrous strands (FIG. 13). Adaxial fibers commonly in contact with adaxial epidermis, abaxial fibers rarely interrupting hypodermis and in contact with abaxial epidermis. VASCULAR BUNDLES (veins) either compound and situated in prominent ribs (FIG. 21) or smaller, simple and not producing pronounced ribbing of lamina (FIG. 18), with a complete transition between infrequent large ribs and numerous small vascular bundles (FIGS. 18–21). Vascular bundles independent of and equidistant from surface layers except largest bundles continuous with abaxial epidermis. Bundles each

with a continuous uniseriate outer parenchymatous sheath of colorless, tabular cells elongated somewhat along the vein; outer sheath incomplete below larger veins. Inner sheath of somewhat thicker-walled cells, uniseriate and indistinct in smaller veins, more pronounced in larger bundles and including lignified abaxial fibers forming a distinct phloem sheath. Fibrous phloem sheath best developed in largest ribs. Largest veins including adaxial sheathing fibers (FIGS. 20, 21). Vascular tissues reduced in smaller veins (FIG. 13); collateral with a wide metaxylem vessel in larger veins (FIGS. 18, 22), large veins with several separate phloem strands (FIGS. 19, 20); largest veins compound with additional lateral vascular bundles resembling isolated small veins of lamina (FIGS. 21, 23). Protoxylem well developed only in larger veins; phloem of smaller veins often divided into two incipiently separate strands by a narrow medium sclerotic isthmus. TRANSVERSE COMMISSURES at irregular intervals connecting longitudinal veins; each with very reduced vascular tissues sheathed by uniseriate slightly sclerotic parenchyma (FIG. 15). MARGINAL RIB including a broad, compound vascular bundle representing fusion product of major longitudinal veins (FIG. 11). CELL CONTENTS not well preserved, no crystalline deposits observed. STEGMATA (silica cells) abundant next to mesophyll and vascular fibers, each with a massively thickened basal wall enclosing an irregularly spherical, spinulose silica body (FIGS. 16 and 17). Bodies 9–12μ wide in stegmata next to veins; smaller, 5–7μ wide next to mesophyll fibers.

Leaf axis (petiole) (FIGS. 26–29). HAIRS common abaxially, resembling those of lamina. EPIDERMIS shallow, outer wall somewhat thickened, wholly cutinized; cells more or less rectangular in surface view, slightly elongated. Abaxial epidermis somewhat papillose towards margin. STOMATA occasional. GROUND PARENCHYMA uniform, cells compact, somewhat elongated; only hypodermal layers slightly modified. Abaxial hypodermal ground parenchyma somewhat sclerotic; adaxial ground parenchyma cells somewhat anticlinally extended, thin-walled, their walls plicately collapsed in a concertina-like manner. Hypodermal ground parenchyma including small fibrous or fibro-vascular strands (e.g. FIG. 27). VASCULAR BUNDLES in two distinct series: (1) Single ADAXIAL SERIES of large INVERTED mostly compound bundles (FIGS. 26, 27), each including a large vascular strand towards the center of the petiole, the vascular tissues with inverted orientation, and one or more small strands embedded in the most fibrous part of the bundle towards the outer surface of the petiole; the vascular tissues of these supplementary strands with oblique or inverse orientation and often represented by phloem alone. (2) Remaining bundles with normal orientation occupying bulk of petiole, divisible into: (a) ABAXIAL SERIES of alternately large and somewhat smaller bundles each with a massive fibrous phloem sheath, the largest bundles compound and including one or more supplementary strands of vascular tissue, often phloem alone, within the fibrous sheath (FIG. 28); (b) CENTRAL SERIES of uniformly constructed bundles with normal orientation,

more or less irregularly arranged but forming two distinct horizontal series in adaxial part of petiole (FIG. 26). Each bundle (FIG. 29) simple with a smaller fibrous sheath than in superficial bundles, including well developed protoxylem, usually two wide metaxylem vessels; the phloem subdivided into at least two separate strands by a medium sclerotic isthmus. Bundles of adaxial and remaining series partially fused in leaf margin to form a large commissure. TRANSVERSE COMMISSURES connecting longitudinal bundles occasional throughout petiole. Stegmata, crystals as in lamina.

Stem.[3] PERIDERM formed by suberisation of outer layers augmented by etagen meristematic activity in outer cortex. CORTEX narrow, up to 2 mm. wide including numerous narrow fibrous strands transitional internally to larger strands including either phloem or both xylem and phloem tissues. No distinct limiting layer for inner cortex. CENTRAL CYLINDER with peripheral congested vascular bundles, each bundle with well developed fibrous phloem sheath, the bundles often somewhat rhombohedral in transverse section. Obvious leaf traces frequent. Central vascular bundles somewhat less congested but with scarcely reduced fibrous sheaths. VASCULAR BUNDLES (FIG. 32) almost invariably with one wide metaxylem vessel, with or without protoxylem; two vessels appearing in bundles close below their exsertion as leaf traces. GROUND PARENCHYMA cells slightly thick-walled, conspicuously pitted, including abundant starch. Stegmata abundant next to vascular fibers (FIG. 34).

Secretory and conducting cells. RAPHIDE-SACS infrequent in all parts. STEGMATA (silica cells) abundant next to fibers in all parts, silica bodies smallest (5μ diameter) in cells next to mesophyll fibers of lamina, largest (12μ diameter) in cells next to vascular fibers of stem. STARCH abundant in ground parenchyma of stem; grains simple, more or less spherical, up to 15μ diameter. VESSELS present in metaxylem of stem, rachis and large ribs of lamina; larger elements in leaf mostly more than 2 mm. long, 70μ wide with scalariform perforation plates with many thickening bars (FIGS. 30, 31) on oblique or very oblique end walls; elements in stem (FIG. 33) average 860μ long, 120μ wide with scalariform perforation plates with 4–10 thickening bars on slightly oblique or oblique end walls. SIEVE-TUBES in stem with slightly oblique compound sieve-plates coinciding with vessel-element end walls; diameter 15–20μ.

DISCUSSION

A limited amount of information on vegetative anatomy of some other genera of Geonomeae: *Calyptrogyne*, *Calyptronoma*, *Geonoma*, *Pholidostachys* and *Welfia* is available in Tomlinson (1961), and suggests that the group shares a few diagnostic anatomical features. Most distinctive is the filamentous uniseriate (rarely biseriate) hair, commonly restricted to

[3] General stem construction corresponds to that described for *Rhapis* by Zimmermann and Tomlinson, 1965.

costal regions and most frequent on the abaxial surface of the lamina. Those illustrated for *Aristeyera* (FIGS. 9, 10, 24 and 25) are quite typical. Hairs are more uniformly dispersed in *Calyptrogyne* and *Welfia*. Those in *Calyptronoma* and *Welfia* are somewhat distinctive in being sunken and this is associated with enlargement of the basal cell. Elsewhere in palms uniseriate filamentous hairs are rare. They occur in the bactroid palms which on morphological and anatomical grounds, however, show no special affinity with the Geonomeae. *Reinhardtia* and *Sclerosperma* may have hairs somewhat similar to those in *Calyptronoma* and *Welfia*.

Other anatomical features which are common to those geonomoid palms which have so far been examined and which are illustrated for *Aristeyera* above are: (1) shape of epidermal cells which are always thin-walled except in *Calyptronoma*, (2) structure and distribution of stomata, (3) structure and distribution of stegmata and to a certain extent the structure of assimilating mesophyll, veins, and ribs. The degree of differentiation of hypodermal mesophyll layers as specialized colorless layers varies from: (1) *Welfia* with a distinct 2-layered colorless hypodermis below each surface, to (2) *Calyptronoma* and, less conspicuously, *Pholidostachys* with a 1-layered hypodermis below each surface, to (3) *Aristeyera* with a 1-layered abaxial hypodermis, to (4) *Calyptrogyne* and *Geonoma* with no colorless hypodermis. Non-vascular fibers vary in their distribution. They are (1) absent from some *Geonoma* species, (2) solitary or in small strands scattered more or less throughout the mesophyll as in *Aristeyera*, *Calyptrogyne*, *Calyptronoma*, and some *Geonoma* species, (3) infrequent as small strands in a single series in *Pholidostachys*, and (4) distinctive in *Welfia* as large strands pectinating with the vascular bundles. Mesophyll fibers throughout the alliance tend to be septate, unlignified and with a wide cell lumen.

It is quite clear, therefore, even from the limited information available, that although the members of the Geonomeae share some common features they are anatomically quite diverse. *Welfia* seems rather isolated. *Aristeyera* shows no special anatomical affinity with *Welfia* although these two genera are most alike in floral morphology. Without further information on many more species of this tribe further speculation about generic affinity on an anatomical basis is pointless.

Nevertheless, the above account has demonstrated that there are anatomical features of diagnostic value in this tribe and continued investigation should reveal more. In view of the size of this assemblage, in the region of 200 species according to Dr. Moore, and considering the small sample for which anatomical information is available (about 10 species and for these mostly fragments of the lamina), one feels justified in stating that the anatomy of the Geonomeae is largely a *terra incognita*.

SUMMARY

A description of the anatomy of lamina; petiole and stem of *Aristeyera spicata* based on small fragments from the collection *Steyermark 90010*

supplements the formal taxonomic treatment and the account of floral anatomy. *Aristeyera* shows anatomical features which hitherto have appeared to be diagnostic for the Geonomeae. Without information about many more species from this tribe it is impossible to comment on the affinities of *Aristeyera* from an anatomical point of view except that it shows less resemblance to *Welfia* than to other geonomoid genera.

LITERATURE CITED

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ZIMMERMANN, M. H., & P. B. TOMLINSON. 1965. Anatomy of the palm, *Rhapis excelsa* 1. Mature vegetative axis. Jour. Arnold Arb. **46:** 160–180. 1965.

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EXPLANATION OF PLATES

(The abbreviations used on the figures are cited here with their equivalents: chlor. = chlorenchyma; exp. = expansion cells; f. (solid black) = fibers of bundle sheaths; hyp. = hypodermis; mes. f. = mesophyll fibers; mxy. (open circles) = metaxylem; phl. (dotted) = phloem; pxy. (open circles) = protoxylem; sc. par. (lined) = sclerotic parenchyma of bundle sheath; scl. = sclerenchyma; xy. = xylem; xy. par. (white) = xylem parenchyma.)

PLATE I

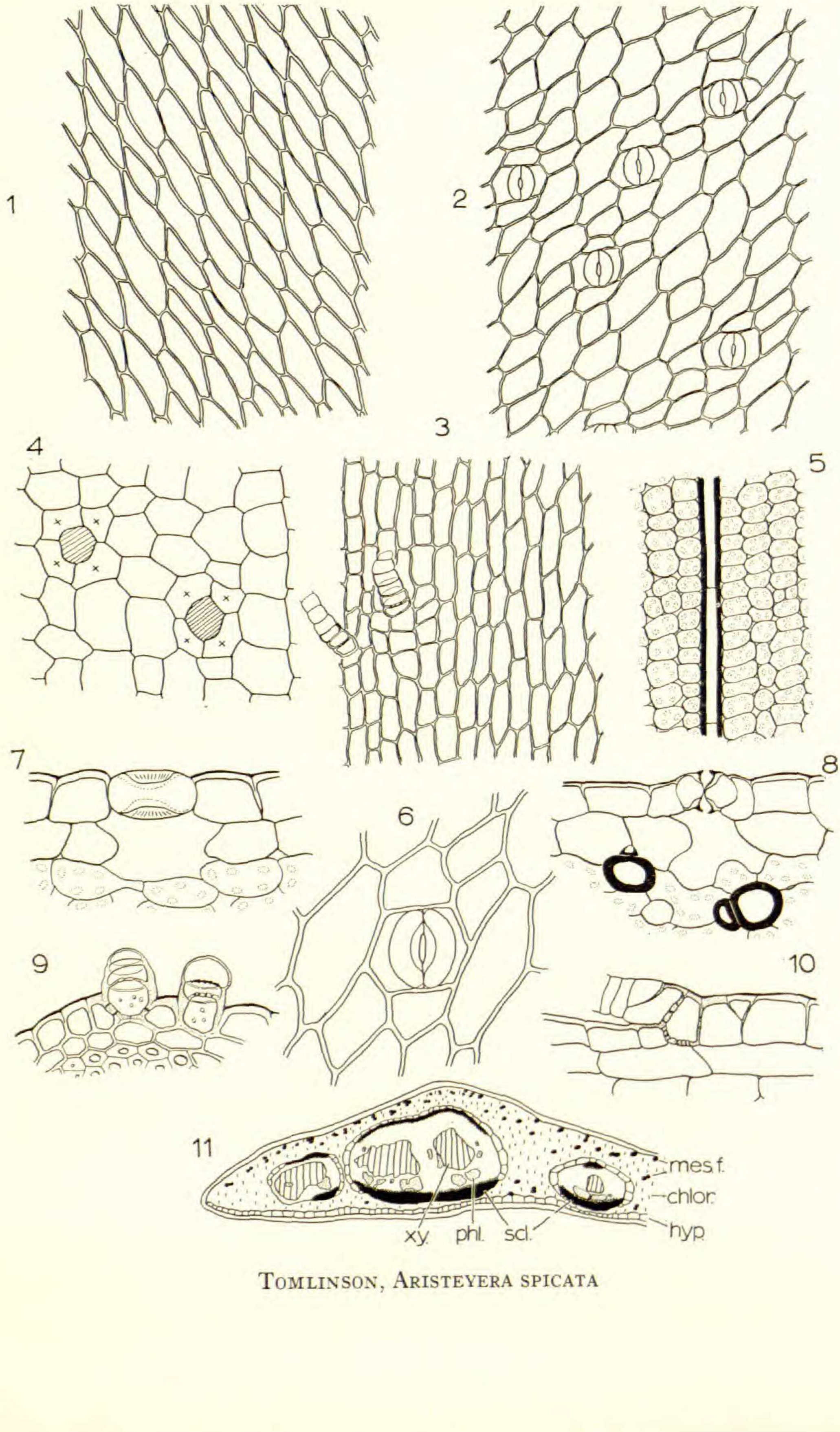
FIGURES 1–11, Lamina of *Aristeyera spicata*. FIGS. 1–5, Surface views, × 220. FIG. 1, Adaxial epidermis. FIG. 2, Abaxial epidermis, intercostal region. FIG. 3, Abaxial epidermis, costal region. FIG. 4, Abaxial hypodermis. FIG. 5, Adaxial mesophyll, hypodermal layer. FIGS. 6–8, Stomata, × 440. FIG. 6, Surface view. FIG. 7, Longitudinal section. FIG. 8, Transverse section. FIGS. 9 and 10, Abaxial hairs, × 440. FIG. 9, Transverse section. FIG. 10, Longitudinal section. FIG. 11, Lamina margin, transverse section, × 32 (cf. FIGS. 18–21).

PLATE II

FIGURES 12–25, Lamina of *Aristeyera spicata* (continued). FIG. 12, Transverse section, × 32, diagrammatic representation of the distribution of veins (solid black). FIG. 13, Transverse section, × 220, enlargement of portion of FIG. 12, inset showing details of cuticle. FIG. 14, Longitudinal section, × 220. FIG. 15, Transverse commissure, × 220, in transverse section from longitudinal section of lamina. FIGS. 16 and 17, Stegmata, × 440, next to isolated mesophyll fibers. FIGS. 18–21, Transverse section, × 32, of veins of increasing size; vascular and mesophyll fibers shown in solid black, xylem lined, phloem dotted, chlorenchyma as short lines. FIG. 22, Transverse section of vein, × 220, enlargement of vein shown in FIG. 18. FIG. 23, Transverse section of small vascular bundle, × 220, enlargement of small lateral bundle from FIG. 21. FIGS. 24 and 25, Hairs shown in surface view, × 440. FIG. 24, Abaxial hair. FIG. 25, Adaxial hair.

PLATE III

FIGURES 26–34, Petiole and stem of *Aristeyera spicata*. FIGS. 26–31. Petiole. FIG. 26, Transverse section, × 6, incomplete, complete outline indicated by dotted line. Inverted bundles shown in solid black, normally oriented bundles lined. FIGS. 27–29, Enlarged details, × 60, of vascular bundles from FIG. 26. FIG. 27, Adaxial, inverted bundles. FIG. 28, Abaxial bundle. FIG. 29, Central bundle. FIGS. 30 and 31, Metaxylem vessel element. FIG. 30, Outline of end wall, × 80. FIG. 31, Details of perforation plate, × 440. FIGS. 32–34, Stem. FIG. 32, Transverse section of peripheral vascular bundle, × 60. FIG. 33, Metaxylem vessel elements from stem, × 80, perforations seen directly represented by solid black; perforations seen through an imperforate wall represented by lines. FIG. 34, Stegmata next to stem fiber, × 440.



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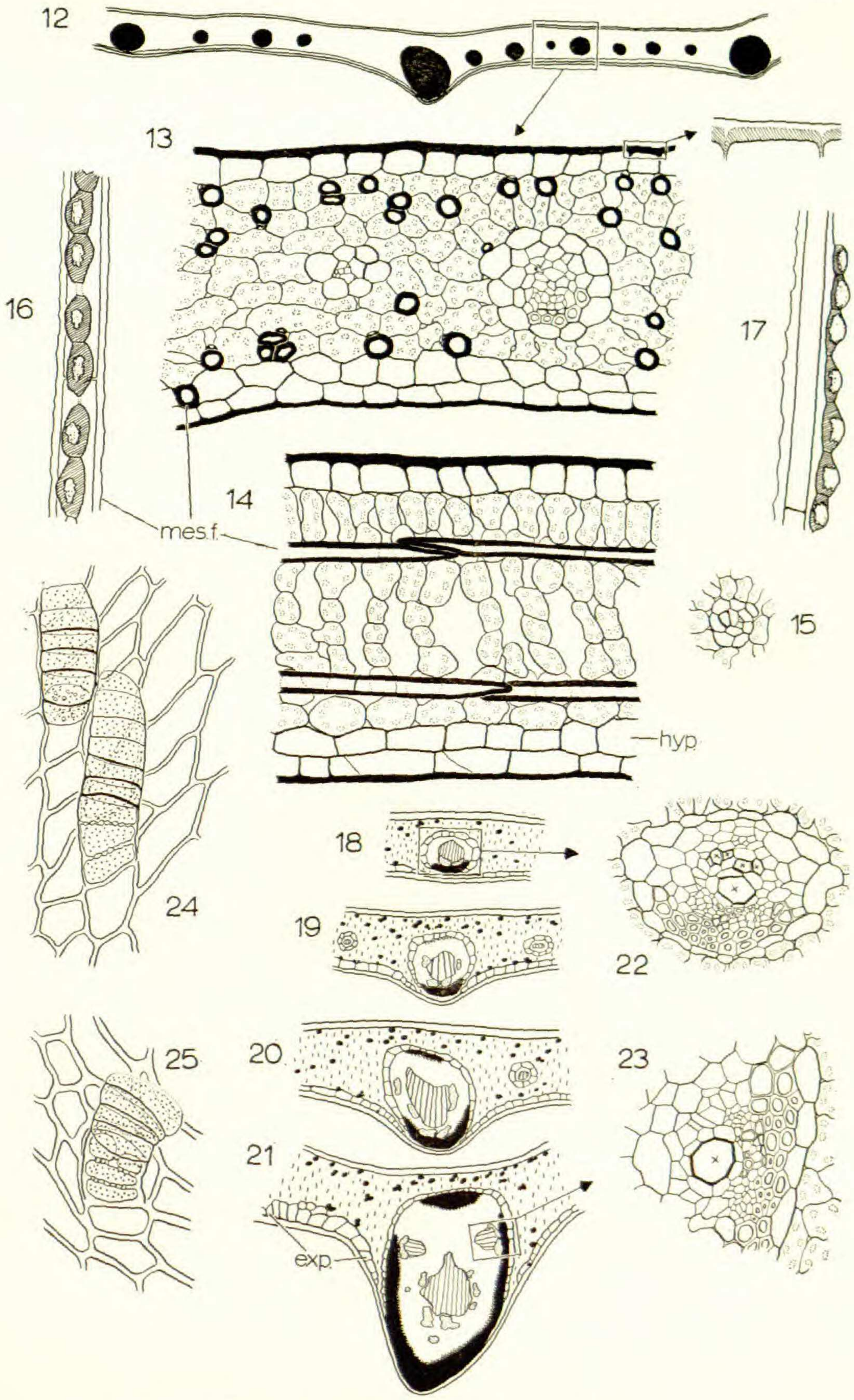

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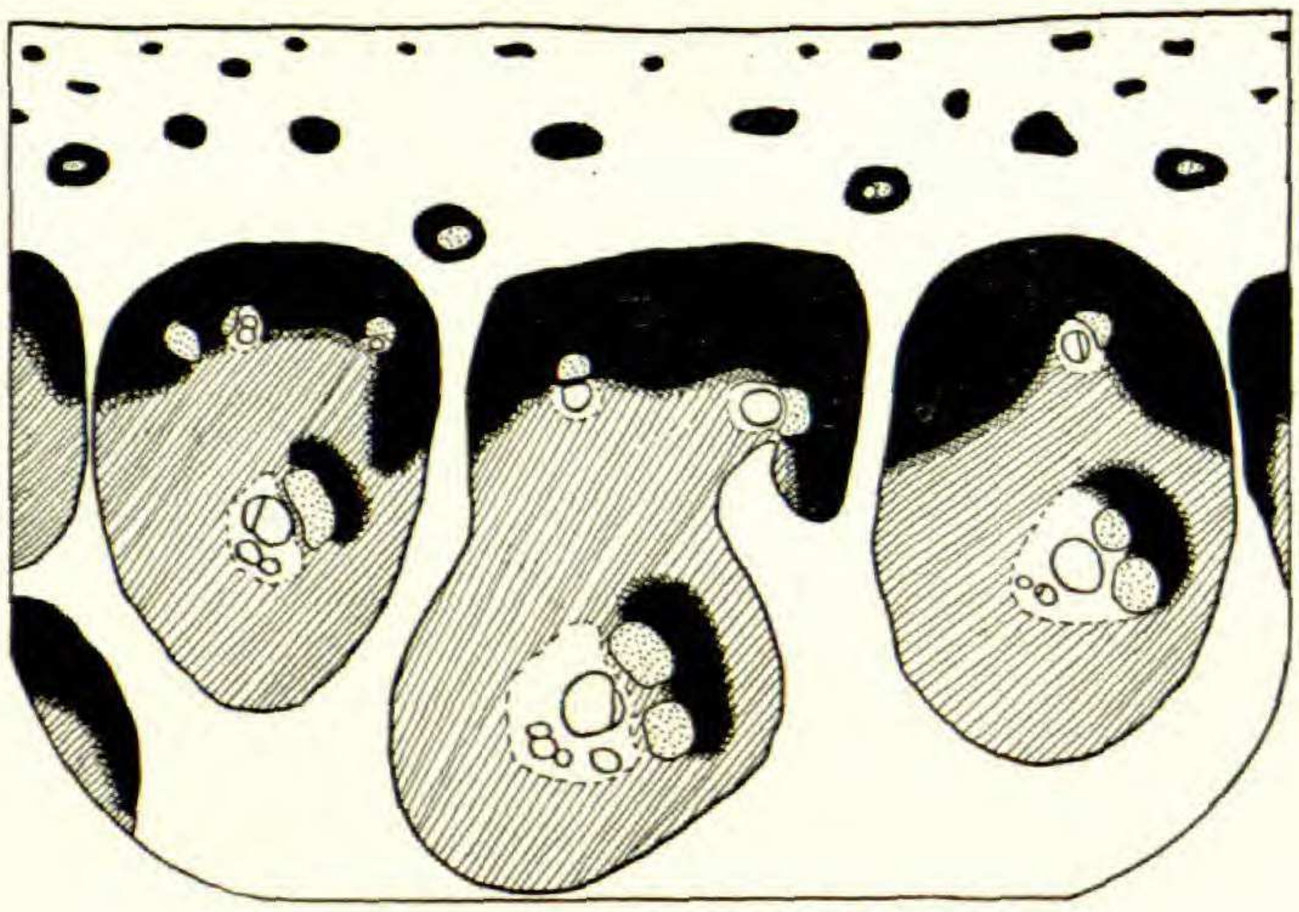
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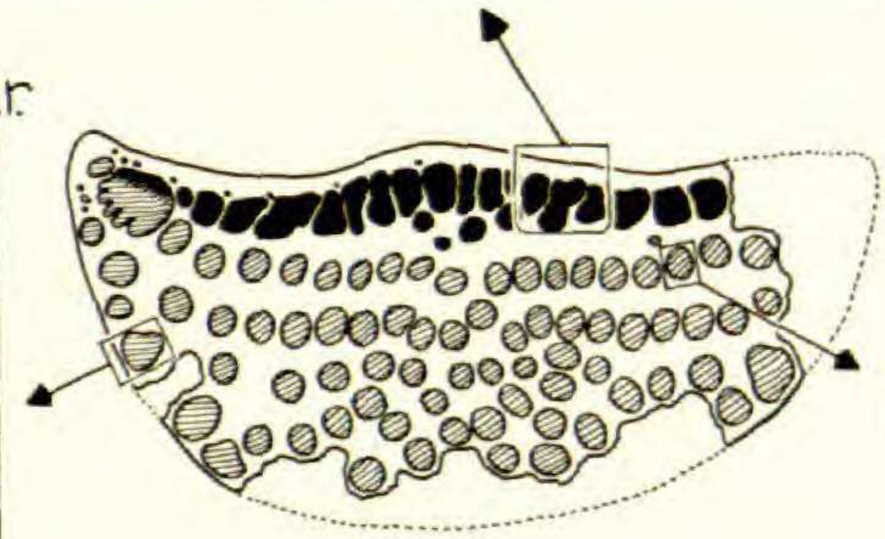
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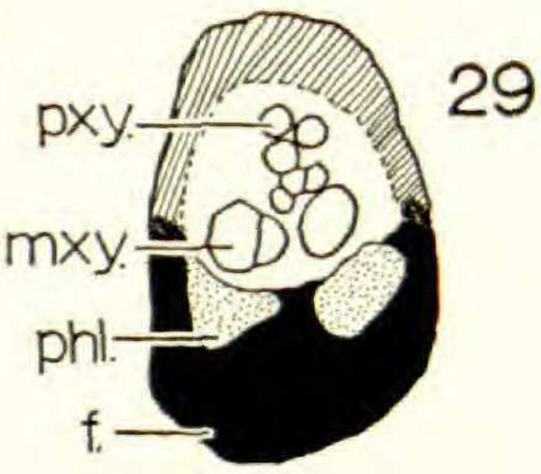

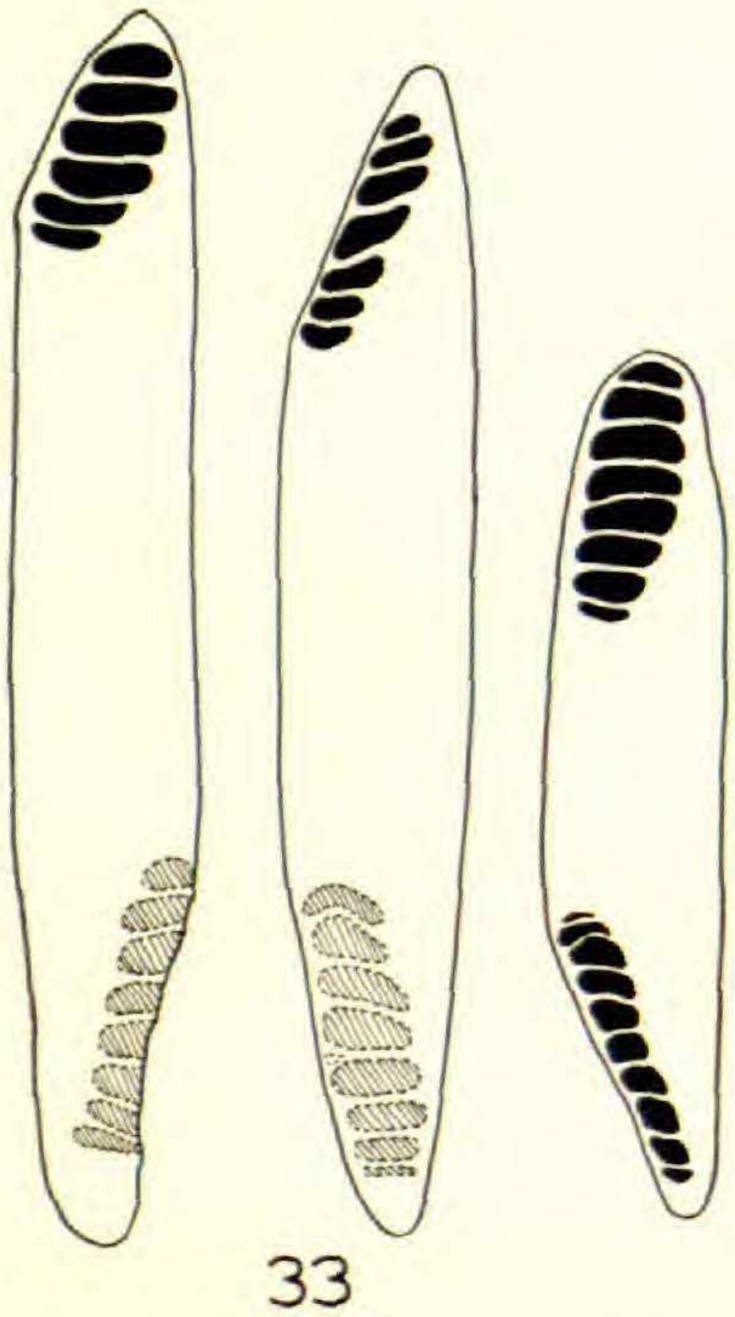
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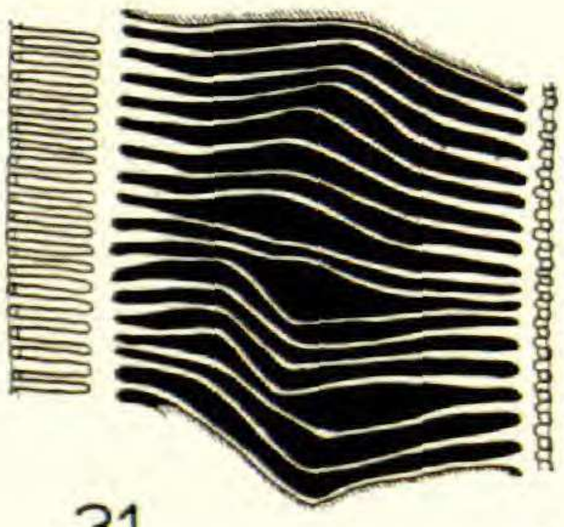
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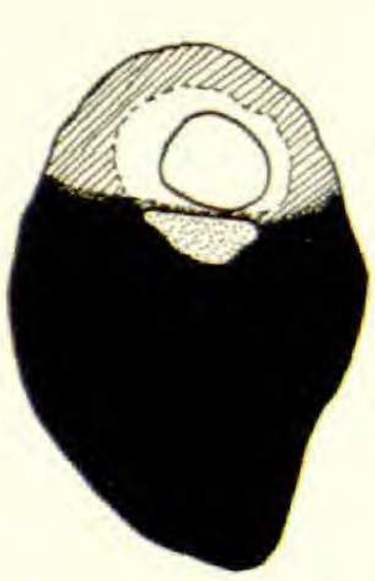
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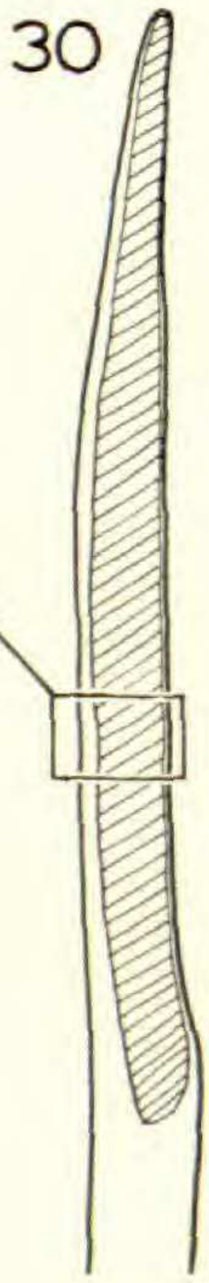
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